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Estimating carbon storage and flux in sea urchin barrens following kelp forest collapse

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ABSTRACT

Mitigating climate change impacts due to excess carbon dioxide will require knowledge of blue carbon sources and sinks. Marine ecosystems including seagrass meadows, mangroves, salt marshes and kelp forests store organic carbon while inorganic carbon is bound as calcium carbonate ($CaCO_3$) in shells. Kelp forest ecosystems however can shift from carbon bound in kelps to sea urchin barrens composed of $CaCO_3$. We examine this ecosystem shift with respect to carbon by estimating purple, *Strongylocentrotus purpuratus*, and red sea urchin, *Mesocentrotus franciscanus*, population abundances (in 2022-2023) in northern California. In these rocky habitats (25,400 Ha), we estimate there are 5.8 billion purple and 577 million red sea urchins in northern California. This conservative estimate results in an estimated 98,000 t of $CaCO_3$ for a total of 11,800 t carbon (46 g C/m^2) in these sea urchin barrens. Sea urchin calcification releases an estimated 30,171 t carbon dioxide (CO_2) while the eventual dissolution results in the uptake of an estimated 43,000 t CO_2 (or 11,800 t carbon). More research is needed to quantify $CaCO_3$ storage/flux, source/sink dynamics, carbon sequestration and the potential for CO_2 removal given ecosystem shifts from kelp forest to sea urchin barrens.

1. Introduction

Climate change brought on by excess carbon dioxide (CO_2) from burning fossil fuels is adversely impacting natural systems that sustain life on the planet. Current estimates suggest we must not only slow CO_2 emissions but also remove 100-900 Gt of CO_2 if we are to keep warming below 2° C (IPCC 2018). This makes it imperative that we learn more about global carbon stores and fluxes. Carbon can be sequestered in persistent carbon sinks such as terrestrial forests (Pan et al., 2011; Grassi et al., 2017) or blue carbon marine and coastal habitats (Smith, 1981; Nellemann et al., 2009). The focus of blue carbon has been on accreting ecosystems such as marsh, mangrove and seagrass beds due to their increased carbon burial rates and accumulation of carbon in tissues and surrounding soft sediments (Macreadie et al., 2021; Howard et al., 2023). Recent work has shown marine ecosystems such as seagrass habitats can sequester similar amounts of carbon per m^2 per year compared with terrestrial forest ecosystems (Eger et al., 2023), (but see, Kristensen et al., 2025). Blue carbon systems envisioned today are mostly small in scale with the exception of marine sediments (Howard et al., 2023). The small size of known blue carbon pathways limits their mitigation capacity to <1% of the 2014 global fossil fuel carbon emissions (Taillardat et al., 2018). Given that the oceans occupy >70% of the earth's surface, we must work to understand blue carbon cycling and identify novel blue carbon mitigation pathways if we are to develop a portfolio of blue carbon sequestration strategies to address the current global warming crisis.

Work on blue carbon has recently recognized the potential contributions of kelp forests for carbon sequestration (Krause-Jensen and Duarte, 2016) calling them emerging blue carbon pathways (Howard et al., 2023). Kelps are fast-growing, highly productive,

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habitat-forming organisms with large standing stocks of organic carbon produced during photosynthesis (Filbee-Dexter and Wernberg, 2020). Kelp can sequester carbon when a portion (10-15%) of the algal biomass is exported to cold deep-water carbon sinks where the carbon can persist for more than 100 years (Hurd et al., 2024; Filbee-Dexter et al., 2024). It is estimated that kelps may be sequestering 5M t per year (Eger et al., 2023) or 150-200 M t per year (Duarte et al., 2022). Kelp forests however are susceptible to dramatic ecosystem shifts tipping from kelp forest to sea urchin barrens (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015), where sea urchins dominate the ecosystem and the carbon in these ecosystems is in the form of inorganic calcium carbonate ($CaCO_3$).

One of the most poorly understood aspects of the carbon cycle in blue carbon ecosystems is the role of inorganic carbon, which has been called the "white elephant in the blue carbon room" (Macreadie et al., 2017). While calcification and creation of inorganic shell ($CaCO_3$) may seem like CO_2 is being removed from the ocean, the calcification process actually releases CO_2. This is because the calcification process rapidly depletes net alkalinity which reduces seawater's CO_2 buffering ability shifting the carbonate chemistry such that the remaining bicarbonate ions are converted into dissolved CO_2 gas. Therefore, production of shell via calcification results in the release of CO_2 (Arrhenius, 1896). Said another way, calcification in seawater increases pCO_2 by depleting CO_3^{2-} thereby reducing total alkalinity (Macreadie et al., 2017). For every mole of calcium carbonate produced during calcification, Dissolved Inorganic Carbon (DIC) is reduced by 1 mol and Total Alkalinity by 2 mol which depletes alkalinity, drives the system to higher *p*CO2 levels and CO_2 is released to the ocean or atmosphere (Frankignoulle et al., 1994; Zeebe and Wolf-Gladrow, 2001). The calcium carbonate cycle consists of CO_2 production during calcification and then absorption during shell ($CaCO_3$) dissolution (Fodrie et al., 2017). Shell dissolution will be enhanced through mechanical wave and surge action physically turning the shell into shell mash. The mash could then be buried in marine sediment layers. Alternatively, low pH conditions could also speed up dissolution. When dissolution does takes place and the shells dissolve or break down, CO_2 is taken up from the ocean and ultimately the atmosphere (Bellamy et al., 2012; Macreadie et al., 2017).

Little work has been done estimating carbon in sea urchin tests, yet sea urchins are capable of dominating nearshore ecosystems transforming them into urchin barrens. Sea urchins can undergo population explosions leading to severe overgrazing driving the conversion of productive, species-rich, algal forests to barren grounds dominated by sea urchins (Lawrence, 1975; Hagen, 1983; Rogers-Bennett, 2013). Sea urchin barren habitats have existed for hundreds of years, identified in Japan as "Isoyake" (Fujita, 2010; Graham, 2010) and are now expanding globally. Like many regions around the world, northern California, bull kelp, *Nereocystis luetkeana,* forests have recently transitioned from kelp forest to sea urchin barrens following a marine heat wave and the loss of a major sea urchin predator; the sunflower star, *Pycnopodia helianthoides* (Rogers-Bennett and Catton, 2019; McPherson et al., 2021). Despite the return of cool water temperatures, sea stars are nearly absent and sea urchin densities remain extremely high. Kelp deforestation by sea urchin herbivory represents a significant loss of carbon sequestration potential (Wilmers et al., 2012). Yet, absent from these discussions are estimates of the amounts of carbon within sea urchin barrens. Sea urchins are long-lived organisms, with red sea urchins, *Mesocentrotus franciscanus*, living for >150 years (Ebert and Southon, 2003). Sea urchins in barren low food conditions can remain at high densities by depressing their metabolism (Spindel et al., 2020) with some sea urchin barrens persisting for decades and centuries. It maybe that the incidence of kelp forest loss and the rise of sea urchin barrens may continue in the future. Calcium carbonate potentially represents a large-scale reservoir in one sub-cycle of the broader global carbon cycle (Smith, 2013). The threat presented by rising levels of CO_2 globally indicates that more information about the blue carbon cycle is needed including the quantity of inorganic carbon as well as inorganic carbon cycling (calcification and dissolution) in sea urchin barrens.

Here we examine the blue carbon cycle in a sea urchin dominated barrens by quantifying the population sizes, $CaCO_3$ content of purple, *Strongylocentrotus purpuratus*, and red sea urchins across 650 km of northern California. We estimate the number of sea urchins on rocky reefs from density surveys following a marine heatwave, massive sea urchin population increase and the standing stock of sea urchins in barrens combining survey data with rocky habitat estimates. We estimate the inorganic carbon content of a wide range of sea urchin sizes to quantify the relationship between sea urchin size and carbon content. We use the abundance and size frequency distribution of the sea urchins to estimate the amount of carbon bound in sea urchins and the amount of CO_2 released during calcification. We examine the potential CO_2 uptake when the sea urchin tests eventually dissolve and quantify the amount of carbon in sea urchin tests in sea urchin barrens (Fig. 1). We discuss how sea urchin removal may benefit kelp restoration and caution that more work is needed before sea urchin removal can be used as a nature based tool for marine carbon dioxide removal (mCDR).

2. Materials and methods

2.1. Density data and subtidal area estimates

Sea urchin data were collected from subtidal surveys using SCUBA transects stratified by depth along Sonoma and Mendocino Counties in 2022 and 2023 as part of the Kelp Forest Monitoring Program of the California Department of Fish and Wildlife and UC Davis Bodega Marine Lab. Sea urchin counts were conducted along 30 × 2 m transects randomly placed within two depth strata: the shallow depths 1-10m and the intermediate depths ranging from 11 to 20 m. Transects were divided into depth strata as sea urchins densities are known to vary by depth. The site locations in Sonoma County were: Fort Ross, Timber Cove, Ocean Cove, and Salt Point. This systematic sampling of the sites was done to force spatial spread thereby helping to reduce spatial autocorrelation. The site locations in Mendocino County were: Van Damme, Russian Gulch, Caspar Cove, and Todd's Point (aka Noyo Harbor) (Fig. 2). Approximately 12 transects were surveyed at each site. Average density estimates for each site surveyed were determined using sea urchin counts per transect area (60 m^2) within each of the two depth strata. The average density for the shallow depth (0-10m), was used to determine the abundance estimate of sea urchins in the shallow depths and the average density for the intermediate deep strata were used to determine the abundance estimates for both the intermediate depth habitats (11-20m) and the deeper depth habitats (21-30m) where no surveys were conducted.

A non-parametric spatial bootstrapping method was used called clustered boot strapping designed to preserve the spatial structure of the density data. The densities were bootstrapped 1000 times for each of the eight survey sites for both purple and red sea urchins at the shallow (0-10m) and intermediate depth (11-20m) habitats to generate an array of densities (8x1000). The subtidal survey transect data (densities as #/m2) were aggregated into eight (8) year/location cluster, e.g., Van Damme 2023. Those were then split into "shallow" and "deep" depth strata, eight groups per stratum. The eight populations of densities were placed in an array of eight (8) rows (year/location groups) each with 1000 columns (densities). That process was performed for both of the depth strata. Each year/location cluster contained density data (#/m2) for "n" number of transects. That "n" was used in a "do loop" to randomly select 1000 densities from the "n" population of densities for the transects in each year/location cluster. The value of each randomly selected density was between the lowest and highest of the densities, from each cluster, creating a "bootstrapped" population for each cluster. The statistics for each group and depth stratum were calculated from these clustered bootstrapped densities.

The overall mean densities for both species of urchin for both depth strata were derived from that array. To estimate the population of red and purple urchins on the north coast, we took the mean of the

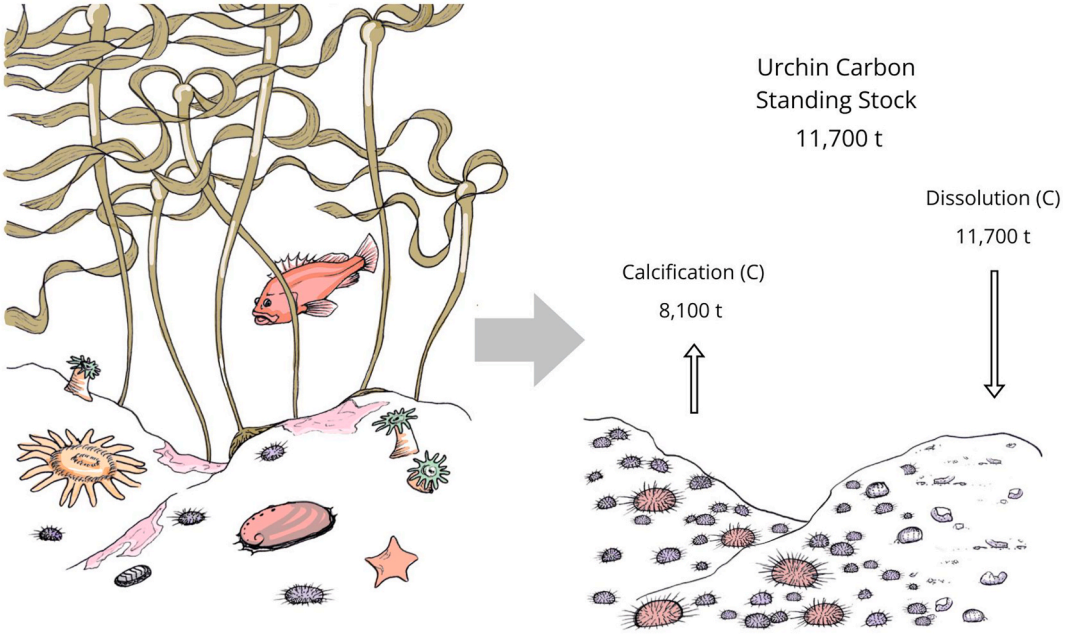

Fig. 1. Illustration of purple and red sea urchin barrens with estimates of carbon bound in sea urchin shells along the coast of northern California. The process of calcification liberates carbon and so this includes estimates of carbon released. Illustration L. Bennett.

bootstrapped densities for sites in Sonoma County (n = 4000) at both depth strata, and the same for Mendocino County (n = 4000). The mean densities at the depth strata were applied to other counties in the north coast by multiplying by the area of rocky habitat. The Sonoma County mean densities were applied to Sonoma and Marin counties, while the Mendocino County mean densities were applied to Mendocino, Humboldt and Del Norte counties. Those estimates were totaled by depth stratum to provide north coast population estimates for shallow, intermediate and deep habitats.

2.2. Subtidal rocky habitat maps

The nearshore rocky subtidal is notoriously challenging to map. The State of California invested resources to support the Marine Protected Area process by mapping rocky subtidal habitats along the northern California coast (Fig. 2). The map layers estimate rocky subtidal reef areas in previously unmapped shallow nearshore waters commonly referred to as the "white zone" (WZ). The zone, where navigational hazards prevent traditional seafloor mapping by vessel, generally extends from the shore out to approx. 10m depth along the coastline (Saarman et al., 2015). This project utilized seafloor and shoreline mapping data from the California's Seafloor Mapping Project (CSMP) and the National Oceanic and Atmospheric Administration (NOAA) Environmental Sensitivity Index (ESI) shoreline habitat categorizations. This project developed subtidal habitat maps in the nearshore WZ using interpolation when there were missing data. After testing different interpolation methods, the three best methods with the highest precision and accuracy across multiple WZ widths were compared. The three methods examined were Inversed Distance Weighting, Tensioned Spline and Natural Neighbor. While all three methods provided estimates, the Natural Neighbor method was ultimately chosen since it was better able to handle clustered and unevenly spaced marine subtidal data without needing a specified search radius.

Using the Natural Neighbor method and geographic information systems software (ArcGIS) subtidal habitat map data depicting the likelihood of rocky reef or soft substrates in the WZ were created (for more detailed methods information see Saarman et al., 2015). These interpolated data are included with the source mapped data provided in maps publicly available through the California Department of Fish and Wildlife (CDFW) mapping and GIS data distribution platform, MarineBIOS (http://www.dfg.ca.gov/marine/gis/viewer.asp). The sea floor maps were then used to determine the total area (m^2) of hard/rocky substrate for each site within three depth strata 0-10m (shallow), 11-20m (intermediate) and 21-30m (deep). Rocky subtidal areas deeper than 30m are not part of this analysis although sea urchins occur at deeper depths.

2.3. Size frequency distribution data

Size frequencies were determined for purple and red sea urchins collected from 1 to 20 m depth in 2016 and 2017 during SCUBA surveys in Sonoma (Timber Cove, Ocean Cove, Salt Point and Sea Ranch) and Mendocino (Van Damme State Park and Todd's Point) counties (Fig. 3). A total of 6595 purple sea urchins from August of 2017 and 2056 red sea urchins from 2016 were measured using vernier calipers to the nearest mm at the widest diameter of the test excluding the spines on the decks of the patrol vessels PV/Steelhead and PV/Marlin and RV/Fulmar.

2.4. Sea urchin age estimates

Estimates of sea urchin age can aid in our understanding of how long the bound carbon may be taken out of circulation in the carbon cycle. We use data and age models from Ebert (2020) to calculate the range of possible ages for purple and red sea urchins. Purple sea urchins have an annual mortality estimate (M) ranging from (0.1 - 0.04), and red urchins have mortality estimates of (0.02-0.2) (Ebert, 2010). We use the formula for time t = ln (0.001)/(-M) assuming an initial cohort of 1000.

2.5. Estimation of calcium carbonate and carbon in urchins

Ninety four purple sea urchin samples ranging from 9.5 to 74 mm were collected from Point Arena, Mendocino County, California in July of 2019. Each sample was placed in an individual plastic container with a 10% bleach solution for 48-72 h to dissolve body tissues from the test, lantern, and spines. This process was repeated until each sample was fully cleaned of tissue. Samples were then rinsed in freshwater and placed in jars to dry for approximately four months in an environment that ranged from 18-24^{0}C before measuring sizes and weights. Desiccant

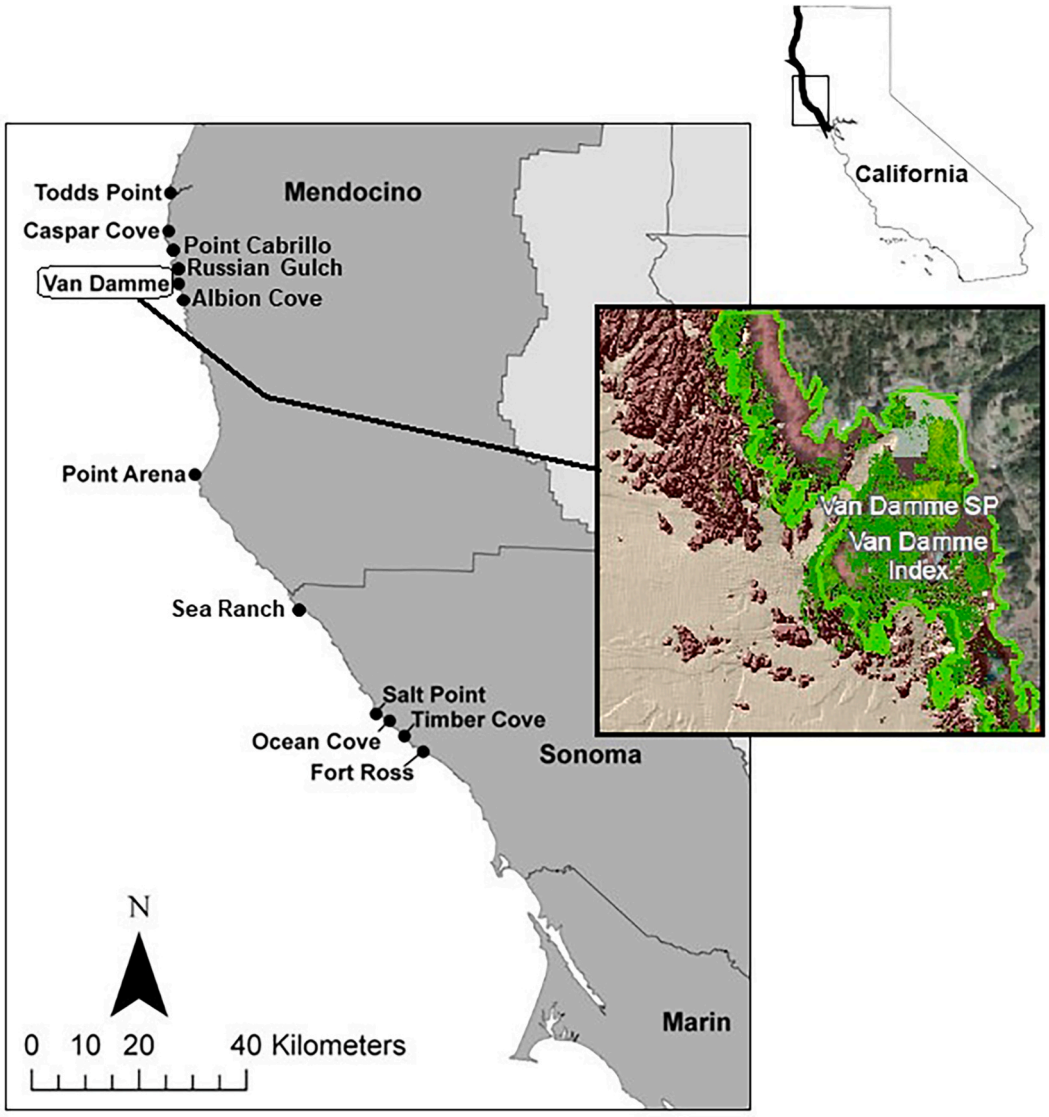

Fig. 2. A map of California with the region of northern California inset to show the study sites were divers assessed the density of sea urchins. A second inset shows the subtidal map of one site Van Damme State Park where the dark orange colors shows the rocky substrate from 0 to 30m depth in as well as the tan soft substrate which is not suitable sea urchin habitat.

packets were used inside sample containers to ensure moisture content was at a minimum during measurements. Each urchin was measured to determine the width of the test excluding the spines (mm), the dry weight of the test (g), and the dry weight of the test, spines and lantern combined ($CaCO_3$ in grams (g). The data were plotted and the exponential relationship between test diameter and the amount of $CaCO_3$ was determined (Fig. 4).

The size categories were divided into 10 mm size bins. The median size for each bin was used to estimate the weight of $CaCO_3$ for that bin size. The abundance of sea urchins in that size bin was multiplied by the median weight of the $CaCO_3$ in the size bin.

This process was repeated for 15 red sea urchin specimens ranging from 32 to 121 mm collected at Port Orford, Oregon in February of 2008 (Fig. 4). The size bins were increased to accommodate the larger sea urchin species. The median weight of red sea urchins within each of the 20 mm size bins was determined using the relationship between size and calcium carbonate and the resulting weight estimate was multiplied by the estimated population for each size bin to estimate the weight of $CaCO_3$ by size bin.

Carbon was calculated as 12% of the $CaCO_3$ weight based on the stoichiometry of 12.02 g/mol carbon to 100.09 g/mol $CaCO_3$.

2.6. Liberation of CO_2 during calcification

Calcification or the production of $CaCO_3$ is a source of CO_2 (Arrhenius, 1896). This is due to calcification increasing pCO_2 by depleting CO_3^{2-} ions, increasing H^+ ions which reduces total alkalinity, thereby releasing CO_2 into the atmosphere (Zeebe and WolfGladrow 2001). For every mole of $CaCO_3$ precipitated (shell created), 2 mol of total alkalinity and 1 mol of Dissolved Inorganic Carbon (DIC) are consumed (Macreadie et al., 2017). Dissolved inorganic carbon (DIC = dissolved CO_2 + HCO_3- + CO_3) is present in the ocean. Specifically, the number of moles of $CaCO_3$ in 100g is 100 g/100.09 g * $mole^{-1}$. We calculate 1.0 * mol of Calcium, 1. 0 * mol Carbon +3.0 * mol Oxygen. The molar mass of $CaCO_3$ is 40 + 12+(16*3) = 100 g/mol, therefore, 100g $CaCO_3$ = 1 mol $CaCO_3$.

For every mole of $CaCO_3$ formed, 0.7 mol of CO_2 are released to the sea/atmosphere (Frankignoulle et al., 1994, 1995; Smith, 2013). In the past, when the oceans were less acidic, the ratio of moles of $CaCO_3$ formed, to moles of CO_2 was lower (0.6 - 0.63) (Ware et al., 1992) and the amount of CO_2 released during calcification was less (Frankignoulle et al., 1994, 1995). Conversely, in the future, as the oceans become more acidic, calcification will release more CO_2 and slightly more than

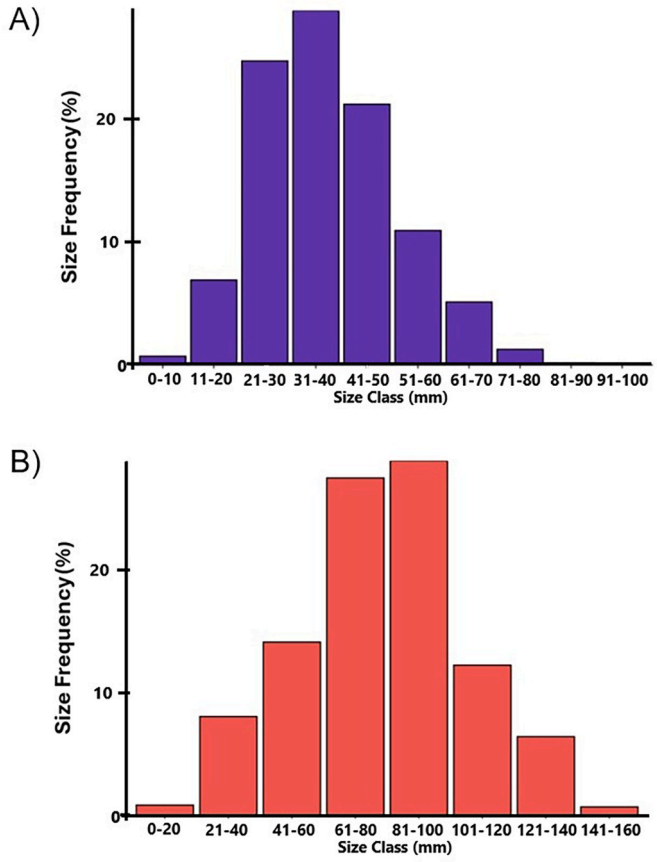

Fig. 3. Size frequency histogram of purple sea urchins (N = 6595) (A top panel) based on sampling from multiple sites along the Sonoma and Mendocino Coast in 2017. Size frequency histogram of red sea urchins (N = 2056) (B bottom panel) based on sampling from multiple sites along the Sonoma and Mendocino Coast in 2016.

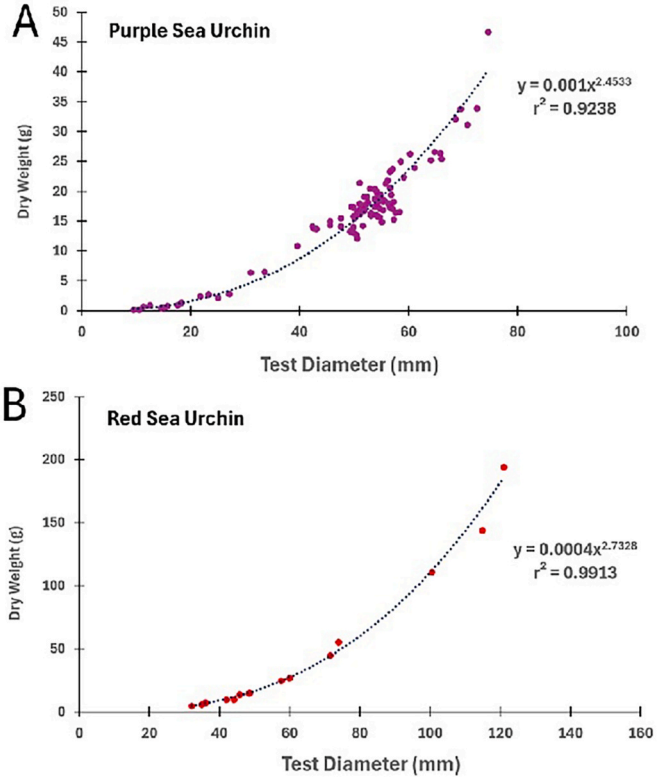

Fig. 4. The relationship between the test diameter (mm) and dry weight of the test, spines and lanterns of (A top panel) purple sea urchins and (B bottom panel) red sea urchins.

0.7 mol of CO_2 will be released for each mole of $CaCO_3$. Therefore, in this paper we use the intermediate value of 0.7 mol of CO_2 released.

2.7. Uptake of CO_2 during dissolution

The process of dissolution of $CaCO_3$ takes up CO_2 from the ocean/atmosphere, which could reduce the net long-term impact of CO_2 liberation from sea urchin calcification. Sea urchins are composed of a high magnesium calcite which is rigid but also very soluble (McClintock et al., 2017). Regional conditions such as temperature and local ocean chemistry such as changes due to upwelling (Takahashi et al., 2014) may influence the eventual draw down of CO_2 from the atmosphere into the ocean's surface waters. This suggests more work is needed on sea urchin test dissolution rates in shallow nearshore oceans. When calcium carbonate dissolves, it reacts with water and CO_2. For this paper we use 1:1 ratio for every molecule of $CaCO_3$ that dissolves one molecule of CO_2 is removed from the solution. Given that the molecular weight of $CaCO_3$ = 100 and the molecular weight of CO_2 = 44, CO_2 is 44% of $CaCO_3$. When the sea urchin dies the dissolution of the test, lantern and spines would take up CO_2 from the atmosphere; (g $CaCO_3$ * 43.97%) = g CO_2 potentially removed. Carbon dioxide has a molecular mass of 44.009 and carbon has a mass of 12.011 therefore we estimate carbon is 27.29% of CO_2.

2.8. Process overview

An overview of the steps in the process for estimating population size, $CaCO_3$, bound inorganic Carbon, CO_2 released during calcification, CO_2 released during respiration and the potential uptake of CO_2 during dissolution is shown in Fig. 5.

3. Results

3.1. Northern California rocky habitat estimates

The subtidal rocky habitat in Marin, Sonoma, Mendocino, Humboldt and Del Norte Counties is estimated to be 254,408,745 m^2 along the approximately 650 km of coastline of northern California (Table 1). This estimate of rocky habitat area is from a depth of 0-30 m. However, sea urchins are known to occur at depths deeper than 30 m but at lesser densities. These data are used to generate conservative estimates of purple and red sea urchin abundances, $CaCO_3$ and C stocks.

3.2. Purple sea urchin populations

We estimate the density of sea urchins at all eight sites in northern California using survey data from 2022 to 2023. We generated an average bootstrapped density for purple sea urchins at the eight sites in shallow habitats and deep habitats (Table 1). In shallow habitats (0-10m) the estimated overall density was 34.83 (95% CI (±) 0.43) purple urchin/m^2 while the intermediate depth (11-20m) density 12.02 (95% CI (±) 0.58 purple urchin/m^2 was used for both the intermediate and deeper depths (21-30m) habitats. This yields an estimated 3,589,624,121 purple sea urchins in shallow (0-10m) water, 1,082,463,431 in 11-20 m depth, and 1,114,064,930 purple urchins in 21-30m water (Table 1). Combining these estimates yields a total purple sea urchin population size in the 0-30m depth rocky habitats along the north coast of 5,786,152,481, or roughly 5.8 billion purple sea urchins (Table 1). This estimate includes the caveat that it does not include purple sea urchin in depths greater than 30 m so this is an underestimate of the standing stock of sea urchins in the region.

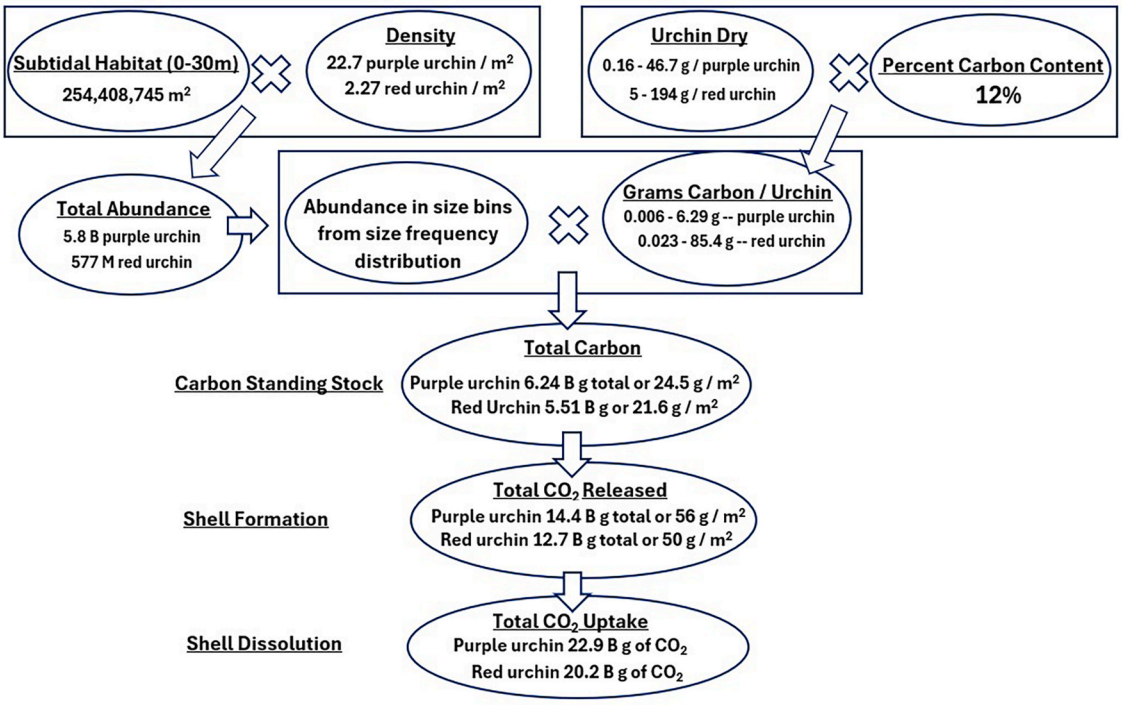

Fig. 5. Flowchart of the procedure used to estimate the total carbon standing stock using sea urchin abundance as well as carbon dioxide released during shell formation and carbon dioxide taken up during shell dissolution.

Table 1
Northern California rocky habitat area estimates, purple and red sea urchin density estimates from Sonoma and Mendocino dive surveys in 2022-2023. The area and density estimates are used to determine purple and red sea urchin population abundances. We use density estimates from the mid depth (11-20m) stratum as the estimate for the deeper depth (21-30m) stratum for each county. Density estimates from Sonoma county dive surveys are used for neighboring Marin County while density estimates from Mendocino County dive surveys are used for Humboldt and Del Norte Counties.

County	Depth Stratum	Rocky Habitat (m^2)	Purple Sea Urchins		Red Sea Urchins		
			Density (#/m^2)	Estimated Population	Density (#/m^2)	Estimated Population	
Marin	0-10 m	16,214,455	31.39	508,999,476	0.64	10,398,870	
	11-20 m	17,183,778	4.98	85,566,487	1.69	29,035,070	
	21-30 m	17,838,162	4.98	88,824,985	1.69	30,140,768	
Sonoma	0-10 m	15,050,167	31.39	472,450,481	0.64	9,652,173	
	11-20 m	10,137,057	4.98	50,477,396	1.69	17,128,373	
	21-30 m	8,680,524	4.98	43,224,602	1.69	14,667,300	
Mendocino	0-10 m	37,368,624	38.28	1,430,369,672	2.31	86,464,906	
	11-20 m	26,619,727	19.06	507,429,235	3.05	81,080,708	
	21-30 m	26,147,886	19.06	498,434,922	3.05	79,643,532	
Humboldt	0-10 m	20,325,236	38.28	777,994,959	2.31	47,029,283	
	11-20 m	13,725,707	19.06	261,641,486	3.05	41,806,966	
	21-30 m	14,599,166	19.06	278,291,486	3.05	44,467,424	
Del Norte	0-10 m	10,445,085	38.28	399,809,533	2.31	24,168,223	
	11-20 m	9,303,716	19.06	177,348,826	3.05	28,338,076	
	21-30 m	10,769,453	19.06	205,288,934	3.05	32,802,549	
		Shallow		3,589,624,121		177,713,456	
		95% CI ±		1.24%		2.48%	
		Mid-depth		1,082,463,431		197,389,193	
		95% CI ±		4.83%		1.60%	
		Deep		1,114,064,930		201,721,571	**Total all urchins**
		95% CI ±		4.83%		1.60%	
		Total		5,786,152,481		576,824,220	6,362,976,702
		95% CI		1.14%		1.48%	1.56%

3.3. Red sea urchin populations

We estimate the bootstrapped overall density of red sea urchins in the shallow habitats (0-10m) of 1.48 (95% CI (±) 0.04) red urchin/m^2 and in the deep habitat (11-30m) 2.37 (95% CI (±) 0.04 red urchin/m^2. (Table 1).This yields an estimated 177,713,456 red sea urchins in shallow water (0-10m), 197,389,193 in the 11-20 m intermediate depth, and 201,721,571 in the deeper water at a depth of 21-30 m (Table 1). Combining these estimates yields a total red sea urchin population size in just the 0-30m rocky habitats along the north coast of 576,824,220 or roughly 576 million red sea urchins (Table 1). This estimate includes the caveat that it does not include red sea urchin in depths greater than 30m, so this is an underestimate of the standing stock of red sea urchins in the region.

Using the methods from Ebert 2010, we find that the range in purple sea urchins' maximum age estimates is from 70 to 173 years and the red urchin are 35 to 345 years old (Ebert et al., 1999). This gives some indication of the number of years carbon will be in situ in the ocean while the animals are living.

3.4. Standing stock of $CaCO_3$

The 10 mm size bin gave the most even distribution of data across each size class for purple sea urchins as determined by examining the size frequency distribution (Fig. 3). The relationship of dry weight (g $CaCO_3$) to test diameter (size) was plotted and curves fitted for each species (Fig. 4):

- Purple sea urchin dry weight ($CaCO_3$) = 0.001 X diameter$^{2.4533}$ ($r^2 = 0.9238$)
- Red sea urchin dry weight ($CaCO_3$) = 0.0004 X diameter$^{2.7328}$ ($r^2 = 0.9913$)

Each purple sea urchin ranged in $CaCO_3$ value of 0.05 g per individual in the smallest size bin (0-10 mm), to 54 g per individual in the largest size bin (81-90 mm) (Fig. 4).

Combining this relationship, the size frequency distribution and abundance, we estimate that the current purple sea urchin population is made up of 52,029 t of $CaCO_3$ (or 22,880 CO_2) with 6242 t of carbon (6.2 bn g). This is approximately 9605 kg of carbon per km of coastline (Table 2).

Using the same methods, with a bin size of 20 mm for the larger-bodied red sea urchins. The 20 mm size bin gave the most even distribution of data across each size class for larger red sea urchins as determined by examining the size frequency distribution. The $CaCO_3$ per red sea urchin ranged from 0.22 g $CaCO_3$ per individual in the smallest size bin (0-10 mm), to 777 g $CaCO_3$ per individual in the largest size bin (161-240 mm) (Fig. 4). We find the red sea urchin population is made up of 45,910 t of $CaCO_3$ (or 20,196 CO_2) and 5514 t of C. This is approximately 8475 kg of carbon per km of coastline (Table 2).

The combined sea urchin populations, both purple and red sea urchins, are estimated to be made up of >97,900 t $CaCO_3$. We determine the CO_2 in this would be 97,700 * 0.44 = 43,076 t CO_2. The standing stock of carbon within sea urchins is estimated at 11,756 t carbon. Along the 650 km of coastline this is 18,081 kg of carbon per km of coastline (Table 2). We find that 11,753 t C per 25,400 Ha. of habitat = 46.3gC/m^2

3.5. Calcification and dissolution and CO_2

Our findings for purple urchins indicate there were 52,000 t of $CaCO_3$, which is a total of 520 M mol of $CaCO_3$. Using the multiplier of 0.7 mol of CO_2 released for every mole $CaCO_3$ equals 328 M mol of CO_2 released. That amount of CO_2 equates to 16,028 t of CO_2 released during calcification. This is 4328 t of carbon released.

For red urchin we determine that there is a total of 45,900 t of $CaCO_3$, which is 459M moles of $CaCO_3$ with 289M moles of CO_2 released. Converting to grams (x 44.01) results in 14.1 bn g (14,143 tons) of CO_2 released during calcification. This is 3819 t of carbon released. When combined, the total purple and red urchin contribution of CO_2 released from calcification is 30,171 t of CO_2 or 8,147t of carbon.

After many years, the sea urchins will die and their tests, spines and lanterns will dissolve leading to the uptake of CO_2. Purple sea urchins have the potential to live for 70-173 years and red sea urchins for 35 to 345 years old. The process of dissolution of 71,700 t of $CaCO_3$ takes up CO_2 from the atmosphere. Given that the molecular wt of $CaCO_3$ = 100 and the molecular wt of CO_2 = 44, CO_2 is 44% of $CaCO_3$. So we find the estimated 97,900 t of $CaCO_3$ * 0.4397 would yield = 43,060 t CO_2 taken up (or an uptake of 11,750 t carbon) when the standing stock of sea urchins die (Fig. 1 and Table 2).

Using purple and red sea urchin abundance estimates, we estimate there is 97,900 t of $CaCO_3$ in sea urchin tests and when this dissolves this would uptake 43,060 t of carbon worth approximately €3.4-4.3M Euros at a rate of €80-100 Euros/t of carbon dioxide (per the EU carbon market in 2023-2025).

Table 2
Estimates of standing stock of tons of $CaCO_3$ and carbon bound in sea urchin barrens in northern California.

	Purple Urchins	Red Urchins	All Urchins
Total t of $CaCO_3$	52,029	45,910	97,938
Total t of Carbon	6243	5509	11,753
Total t of Carbon per Km of Coastline	9.6	8.5	18.1

4. Discussion

4.1. Sea urchin barrens

Marine heatwaves exacerbated by excess CO_2 is a driver in ecosystem regime shifts from species rich kelp forests to sea urchin barrens leading to low species diversity (Arafeh-Dalmau et al., 2020; Smale, 2020). In this case study, there were no sea urchin barrens in northern California prior to the marine heatwave and loss predatory sea stars (Rogers-Bennett and Catton, 2019; McPherson et al., 2021) due to sea star wasting disease (Prentice et al., 2025). Since then, we estimate there are now in excess of 5.8 billion (bn) purple and 577 million (M) red sea urchins in the rocky habitats from depths to 1-30 m. This is a conservative estimate as there are more sea urchins beyond a depth of 30 m. Sea urchin densities continue to increase with these estimates from recent years (2022 and 2023) being higher than at densities at the start of the sea urchin population increase in 2015-2017 (Rogers-Bennett and Catton, 2019). It is unknown how high sea urchin densities will get or for how long they will remain in northern California however, there are regions around the world such as in southern British Columbia (Dawson, 1880; Spindel et al., 2021), Japan (Fujita, 2010) and elsewhere (Ling et al., 2015) that sea urchin barrens have persisted for >140 years.

4.2. Kelp forest restoration

The removal of sea urchins is a nature based restoration strategy that can help restore kelp forests (Miller et al., 2022) where the primary factor limiting kelp recovery is sea urchin overgrazing (McPherson et al., 2021). Kelp forests provide a range of ecosystem services including supporting fisheries for kelp dependent species (Piñeiro-Corbeira et al., 2025) such as abalones, promoting biodiversity and tourism as well as carbon sequestration (Eger et al., 2023). In northern California, where the bull kelp is an annual species, the kelp recruits each year and then the blades produce sori that shed spores onto the benthos. More work needs to be done to determine the longevity of the spore bank for kelp in sea urchin barrens habitats (but see Schoenrock et al., 2021).

Carbon sequestration occurs when portions of the kelp sink into deep cold habitats for more than 100 years (Filbee-Dexter and Wernberg, 2020). This region in particular, the west coast of North America, has one of the world's highest potential rates of kelp carbon sequestration due to the cold water and narrow continental shelf (Filbee-Dexter et al., 2024). Restoration strategies in northern California are focused on targeted sea urchin removal to encourage kelp regrowth in small sections of the coastline (Ongoing Work), aimed at preserving kelp refugia (Cavanaugh et al., 2023), kelp spore production, and kelp genetic diversity (Hohman et al., 2019). Bull kelp in northern California is diverse with high allelic and private allelic richness (Gierke et al., 2023), making this region particularly important for kelp forest restoration. Many regions around the world are engaged in active kelp restoration

through the targeted removal of sea urchins that are forming barren habitats (Tracey et al., 2015; Miller et al., 2022; Eger et al., 2022). Quick lime has also been used to kill sea urchins however, this strategy also kills other echinoderms (Verbeek et al., 2021). Grazer removals are also used either by fishing portions of the urchin stock near kelp (Lee et al., 2021) or by ranching sea urchins fattening them for market (Urchinomics 2020; Angwin et al., 2022). Quantifying of the scale of the sea urchin populations can help inform kelp restoration actions vital for protecting kelp forest ecosystems.

Sea urchin overgrazing can be very destructive to the kelp forest. In northern California, bull kelp forests are now roughly 5% of what they were prior to 2014 (Rogers-Bennett and Catton, 2019) resulting in the loss of carbon sequestration from the kelp forest. The suppression of sea urchins by sea otter predation in the Gulf of Alaska and British Columbia was estimated to protect carbon fixation by kelp thereby preserving 4-8 million t of carbon sequestration (roughly 1 t carbon/Ha) (Wilmers et al., 2012) however fixation may not equal sequestration so this may be an overestimate (Ross et al., 2022). Similarly, sea urchin overgrazing can also lead to seagrass destruction resulting in not only the loss of carbon sequestration but also the remineralization of carbon stored in seagrass beds also triggering methane release (Macreadie et al., 2017a; Hilmi et al., 2021). The destruction of seagrass meadows is estimated to release 12 t carbon/Ha. in southeast Australia (Carnell et al., 2020). While the sequestration of organic carbon by kelp sinking into the deep sea is vastly different than inorganic carbon in sea urchin tests which are subject to complex alkalinity buffering cycles we examine them both since they are alternative stable states of the ecosystem which can shift from one state to the other.

4.3. Carbon in sea urchin barrens

The shift from kelp forest to sea urchin barrens has implications not only for fisheries and biodiversity but also for carbon. Sea urchin barrens are capable of storing carbon in the form of $CaCO_3$ and producing CO_2 through calcification (Fig. 1). The loss of kelp and other vegetated marine ecosystems by sea urchin overgrazing is a triple carbon threat; first the loss of the carbon sequestration provided by the algae/plant (IUCN Blue Carbon, 2017), second the liberation of carbon after ecosystem destruction (habitat conversion) (Pendleton et al., 2012) and third, the release of CO_2 during sea urchin calcification.

Purple and red sea urchins are good examples of organisms that lock away carbon in calcium carbonate for 70-300 years whereas, oyster shell may last only 2-10 years (Powell et al., 2006). In this study, CO_2 is emitted during calcification, and roughly an equal amount of carbon is bound as $CaCO_3$, (Eq. (1)). We note that there will also be carbon released during respiration but that this is typically not included in carbon sequestration accounting due to the short term nature of the release. Further, the carbon released during respiration will go initially into the surrounding seawater rather than the atmosphere until the eventual air/ocean equilibration occurs however, this is notoriously challenging to quantify (Hurd et al., 2024). Nevertheless, sea urchin barrens represent an overall source for carbon rather than a sink (Eq. (1)). Dissolution and sea urchin test breakdown might also contribute to carbon stocks in marine sediments, which have very high carbon content (Atwood et al., 2020). Sea urchins, like corals, are long lived and while they both build $CaCO_3$ skeletons which store carbon for decades, the debate has largely been settled - that corals and bivalves are not considered blue carbon sinks due to the emission of CO_2 during calcification (Ware et al., 1992; Gattuso et al., 1999; Macreadie et al., 2017). We point out that this release of CO_2 during calcification is largely offset by the uptake of CO_2 during eventual dissolution. Corals and sea urchin shell mash may also be contributing to the high carbon content in marine sediment.

These carbon estimates do not account for the loss of carbon sequestration from the kelp forest had the sea urchins not overgrazed the kelp. We estimate sea urchin barrens have 46 g C/m^2 in the barrens areas of northern California. Comparing the carbon content per unit area between sea urchin barrens and kelp forest in the region is challenging given differences in estimates of kelp sequestration. Here we use an estimate for wild bull kelp beds of 82 g C/m^2 (Eger et al., 2023). Even though the estimate for carbon/m^2 in the barrens is roughly half that of kelp, we point out that barrens in this region occupy far more area overall than kelp forests did at their peak, prior to deforestation. In this case study, sea urchin barrens occupy 60 times the area (25,400 ha) compared with the kelp forest (420 ha) when using the highest kelp canopy year in a 35 year times series (McPherson et al., 2021).

The rates of the inorganic carbon cycling will differ with calcification taking place over 2-4 years, with more work needed for dissolution rates which maybe slower. Higher mortality and more dissolution is possible if a lethal urchin disease were to spread through the population as has occurred elsewhere. In the Caribbean and in Oman, mass mortalities occurred in long spined sea urchins, *Diadema antillarium*, caused by a ciliate parasite (Ritchie et al., 2024). Elsewhere balding sea urchin disease has been associated with warm water events and a *Vibrio* bacteria, which also spread quickly (Frederico et al., 2023). Purple and red sea urchins in California have succumbed quickly to disease events in the past (Pearse and Hines, 1987) however, the etiology of the disease is uncertain. Another echinoderm the sunflower sea star has suffered mass mortalities due to another *Vibrio* bacteria (Prentice et al., 2025) in California and Baja California Mexico. If a mass mortality of sea urchins occurred in northern California, there would be widespread rapid calcium carbonate dissolution with an uptake of CO_2 from the surrounding seawater and eventual equilibration with the atmosphere.

4.4. Marine carbon dioxide removal

There is a growing interest in developing strategies for marine carbon dioxide removal (mCDR) (Mannion et al., 2023; Howard et al., 2023) to help mitigate greenhouse gas emissions (IPCC AR6, 2023; Doney and Lubchenco 2023. We caution that more work needs to be done in this field before any strategies should be implemented. An array of mCDR strategies have been proposed however including nature based solutions; restoration of coastal habitats that are carbon sinks such as kelp forests as well as technology-based solutions such as ocean alkalinity enhancement (OAE)/enhanced weathering (Renforth and Henderson, 2017; Bach et al., 2019; Li et al., 2025), and electrochemical or photochemical removal of CO_2 (Doney and Lubchenco, 2023). The mCDR concept of the OAE is to add alkaline substances to the ocean to convert dissolved inorganic CO_2 into dissolved bicarbonate ions and solid carbonates that have a long life. One strategy proposed for OAE is the mining of terrestrial alkaline minerals including carbonates and silicates and dissolving them in the ocean or spreading on the seashore (Oceanvisions.org). The CO_2 from the atmosphere would then eventually be absorbed back into the ocean's surface waters to restore equilibrium. The $CaCO_3$ in sea urchin tests, is an alkaline substance that when added to seawater readily accepts hydrogen ions, enhancing the absorption of CO_2. The $CaCO_3$ when partially dissolved would also buffer ocean acidification while serving as a CO_2 sink (Macreadie et al., 2017; Renforth and Henderson, 2017). The scale of sea urchin barrens, worldwide suggests that $CaCO_3$ from sea urchin removal could be considered as an OAE; 1) provides a source of alkaline material for OAE 2) sea urchin dissolution helps buffer against ocean acidification, 3) dissolution results in the uptake of CO_2 and 4) can be used as a soil amendment “weathering” (Garau et al., 2012).

For sea urchin removal to become an emerging mCDR pathway (Lovelock and Duarte, 2025) it must provide long-term carbon storage, not have deleterious ecosystem effects but still be scalable and cost effective. We suggest that while there are costs to removing sea urchins, $4200-10,700USD/t (S. Semans, Noyo Center for Marine Science, pers. comm.), this cost could be offset by feeding barrens sea urchins (ranching) for 9 weeks to restore their fishery value (Urchinomics™, Angwin et al., 2022). Using purple and red sea urchin abundance

estimates, we estimate there is 97,900 t of $CaCO_3$ in sea urchin tests and when this dissolves this would uptake 43,060 t of carbon worth approximately €3.4-4.3M Euros at a rate of €80-100 Euros/t of carbon dioxide (per the EU carbon market in 2023-2025). Many parameters such as energy prices, regulation changes, and broader economic forces causing volatility in the carbon market including spikes, clustering and asymmetries (Wang et al., 2025).

We point out that there are numerous regions around the world with large and destructive sea urchin barrens (Hagen, 1983; Filbee-Dexter and Scheibling, 2014; Carnell et al., 2020). While sea urchin fishing may be more costly than terrestrial chalk mining for OAE (OceanCDRScience.org), chalk does not have the value added benefits of 1) kelp reforestation, 2) fisheries restoration, 3) enhanced biodiversity and 4) increased coastal tourism as well as 5) the value of the $CaCO_3$. In this case, the challenge will be for sea urchin removal to increase in scale while remaining affordable, proving effective and most importantly preventing negative ecosystem impacts. New methods for quantifying carbonate ocean parameters such as Total Alkalinity, DIC and Carbon using floats and ship based measures are coming online to help us assess conditions (Zhong et al., 2025). We suggest, as others have, that many questions remain about OAE including those of scale, science of OAE, verifying CO_2 removal, as well as economic and ethical considerations that must be addressed *prior* to becoming operational (Ricart et al., 2022; Fujita et al., 2023; Troell et al., 2024).

5. Conclusions

The scale of sea urchin barrens around the world, their destructive overgrazing and the fact that they are predicted to increase in the future ocean suggest that we must learn more about the role of sea urchin $CaCO_3$. as components of the inorganic carbon cycle. Clearly, more work is needed to monitor, quantify and assess the potential of sea urchin $CaCO_3$ as part of a diverse portfolio of kelp restoration and blue carbon mitigation strategies.

Declaration of generative AI use

The authors declare AI was not used in the generation of this manuscript.

CRediT authorship contribution statement

Laura Rogers-Bennett: Conceptualization, Formal analysis, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Sarah Farnsworth Hayroyan:** Conceptualization, Formal analysis, Methodology, Validation, Writing – original draft. **Gabrielle Yang:** Data curation, Methodology, Visualization, Writing – original draft. **Lucille K. Bennett:** Conceptualization, Validation, Visualization, Writing – original draft. **Robert Klamt:** Data curation, Formal analysis, Methodology, Validation, Writing – original draft. **Donald W. Rogers:** Conceptualization, Methodology, Visualization. **Daniel K. Okamoto:** Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

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Data availability

The data that support the findings of this study are available from the NSF-BCO-DMO data collection. Search term: Rogers-Bennett https://www.bco-dmo.org/person/818921.

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